

Leaf Phenology of the Climbing Fern *Lygodium venustum* in a Semideciduous Lowland Forest on the Gulf of Mexico

KLAUS MEHLTRETER

Departamento Ecología Funcional, Instituto de Ecología, A.C., km 2.5 antigua carretera
a Coatepec No. 351, Congregación El Haya, Xalapa 91070, Veracruz, México

ABSTRACT.—Leaf phenology in a population of the climbing fern *Lygodium venustum* was observed during a 31-month period in Veracruz, Mexico. The study site is located 100–200 m from the Gulf coast in the understory of a semideciduous lowland forest dominated by trees of *Enterolobium* and *Ficus*. Four leaf parameters: leaf growth of main and secondary axes, number of living leaves, leaf production and leaf mortality were scored monthly and correlated with two climatic factors: monthly mean temperature and precipitation. Sixty percent of the 37 individuals were supported on lianas, dead wood or shrubs. Smaller, unsupported plants with a height of less than 2.5 m had a mean number of 1.9 ± 0.27 leaves and produced 3.7 ± 0.52 leaves per year and did not become fertile. Over 50 % of the leaves died within the first 3 months, whereas over 10% lived for 12 to 30 months, resulting in a mean leaf life span of 5.6 ± 0.7 months. All leaf parameters were seasonal with the exception of the growth of the main axes. During the rainy season, leaf growth of secondary axes and leaf mortality increased approximately threefold and leaf production rose twofold. Correlations between climatic factors and leaf parameters were strongest within a time lag of one month. The strongest correlation was found between precipitation and the growth of secondary axes, indicating that water is the limiting factor. One to five dormant buds developed on 17.7% of the leaves contributing to 40.3% of the total leaf growth. The potentially long life span of the climbing leaves and the outgrowing dormant buds make this species a successful pioneer in disturbed vegetation and a competitive weed in Mexican vanilla plantations.

Ferns are rarely considered as study organisms for phenological research in the tropics (Mehltreter and Palacios-Rios, 2003), because trees and shrubs are of more commercial interest, and because deciduous tree species are responsible for considerable microclimatic changes within a forest (Lieberman, 1982; Bullock and Solis-Magallanes, 1990; Foster, 1996; Williams-Linera, 1999). On the other hand, ferns and other understory perennial herbs must adapt to the changing microhabitat conditions created by deciduous canopy species. For example, the smaller root system of ferns might have more difficulty accessing water during the dry season. Because ferns are independent of pollinators for reproduction and animal vectors for their dispersal (Barrington, 1993) it might be expected that their rhythms of leaf growth and fertility are primarily responding to seasonal changes in precipitation and temperature.

Prior to the introduction of the Asian species *Lygodium microphyllum* (Cav.) R. Br. into Florida where it has become an invasive weed, there was no published data on the life history of any *Lygodium* species. Recent research on the genus has focused on paleontological (Collinson, 2002), morphological-anatomical (Carlquist and Schneider, 1998), developmental (Mendoza *et al.*, 1998) and physiological aspects (Kurumatani *et al.*, 2001), but no ecological

studies have been published. Consequently, the present contribution represents the first ecological field study in a species of this genus. Its objective was to measure leaf growth, leaf production, leaf mortality and fertility of a natural population of *L. venustum*; to determine their seasonality, leaf life span and the frequency of different orders of ramification; to correlate these results with monthly means of temperature and precipitation; and to relate these findings to a potential weedy character.

Lygodium (Schizaeaceae) is a widely distributed genus of about 35 species, with three native species in Mexico: *L. heterodoxum* Kunze, *L. volubile* Sw. and *L. venustum* Sw. (Mickel and Smith, 2004). *Lygodium venustum* is widely distributed in Latin America, from Mexico to Paraguay and the Caribbean islands, where it grows from sea level to 1100 m elevation. It is one of about 200 climbing fern species (Mehltreter, 2002) with specialized adaptations for a liana life-form. While some ferns (e.g. *Bolbitis bernoullii* (Kuhn ex Christ) Ching, *Lomariopsis recurvata* Fée) climb with their rhizomes and others (e.g. *Hypolepis nigrescens* Hook.) use their spreading leaves to find and hold on to the surrounding vegetation, *L. venustum* is a true climber with a twining rachis. Like those of *L. japonicum* (Thunb.) Sw., the leaves of *L. venustum* are produced from a subterranean rhizome in a heteroblastic series (Mueller, 1982b), i.e. the first juvenile leaves are dichotomously to anisotomously divided and of determinate growth of up to 20 cm (K. Mehltreter, pers. obs). Larger, twining leaves are 3–4 pinnate, of indeterminate growth and can reach a length of 10 m or more. Leaf rachis elongation near the leaf tip is rapid, whereas pinnae expand tardily. The pinnae consist of a short axis bearing two opposite, lateral, pinnate-pinnatifid pinnules and a terminal dormant bud; the latter can develop, in response to injury or destruction of the main leaf tip by herbivores or fungi (Mueller, 1983), into a ramifying leaf blade. Outgrowing buds of the primary pinnae do not enlarge just the pinnae axis to produce more pinnules, rather resume the same morphological ramification pattern as an entire leaf. Consequently, the buds of the primary pinnae become, structurally, a new “rachis” (additional levels called secondary, tertiary, etc. axes to avoid terminological confusion) with new pinnae that again bear leaf buds, but it is unknown how often this ramification can be repeated under natural conditions. The stipe and rachis have a diameter of 1–3 mm and are morphologically unable to thicken secondarily.

MATERIALS AND METHODS

This study was conducted in a semideciduous coastal lowland forest of the Biological Station of La Mancha on the Gulf coast of the state of Veracruz, Mexico (19°36'00"N, 96°22'40"W). The forest canopy, which reaches a height of up to 22 m, is dominated by large individuals of *Brosimum alicastrum* Sw., *Bursera simaruba* (L.) Sarg., *Cedrela odorata* L., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Ficus cotinifolia* Kunth and *Ficus obtusifolia* Kunth. Common species in the middle stratum are *Coccoloba barbadensis* Jacq., *Jacquinia macrocarpa* Cav., *Nectandra salicifolia* (Kunth) Nees, *Piper amalago* L. and

Randia monantha Benth. Lianas, e.g., *Agdestis clematidea* DC., *Paullinia tomentosa* Jacq. and *Vitis bourgaeana* Planch, are frequent, but epiphytes are very rare (Castillo-Campos and Medina A., 2002). The climate is characterized by a mean annual temperature of 25.6°C, a mean annual precipitation of 1198 mm, and a dry season from November to April, when mean precipitation is less than 45 mm per month. A deep, sandy clay soil is developed on old sand dunes (Geissert and Dubroeuq, 1995).

In January 1999, all 37 individuals of *L. venustum* encountered within an area of 150 × 50 m were tagged. Height of the *Lygodium*-plants, the distance from soil to the uppermost part of the plant, was measured with a metric tape or in larger plants with a 12 m telescopic measuring rod. The support type was classified within four categories: no support, liana, shrub, and dead wood. The diameter of the climbing support (i.e. liana, branch, or twig) that was entwined by *Lygodium*-leaves was also recorded. Twenty-two of these 37 plants were chosen for the phenological study because they were accessible by a ladder, i.e. plants that grew nearby to a tree to access the larger leaves without damaging them by leaning a ladder on them, or that were less than 2.5 m high. From February 1999 to August 2001, all new leaves were tagged, counted and measured monthly. Apical and lateral leaf growth of each order of ramification was computed for each plant as the number of centimeters added to all developing leaves between monthly observations. Leaf production was determined as the number of new leaves produced by a plant in one month. Leaf mortality was determined as the number of dead (without green blades) or lost leaves on a plant during one month, counting the mortality of each leaf only once. The mean leaf number for the population was calculated as the average of living leaves per plant. Leaf life span was calculated as the difference between the date of first observation of occurrence and the date of death or disappearance of that same leaf. Monthly leaf production and growth rates were extrapolated by multiplying the results by 30 and dividing by the number of days of each observation period. Linear correlations between monthly means of temperature, precipitation and phenological parameters were tested for their level of significance. Climatic data are from the nearby Biological Station of La Mancha. Statistical analyses were performed with *SigmaStat* (1995). Applied tests and correlations are cited in the text, tables and figure legends. Means are listed with ± 1 SE. Species vouchers (*Mehltreter* 1133, 1134) were deposited at the herbarium of the Instituto de Ecología, A. C. in Xalapa (XAL).

RESULTS

Thirty-seven individuals clumped in 12 groups were found in the study plot of 7500 m² (= 49 plants·ha⁻¹). 40.5% of the plants were less than 50 cm in height and had no support for their climbing leaves (Fig. 1). All larger plants climbed on one of the support categories: woody lianas (24.3%), dead wood, i.e. fallen branches and twigs (24.3%) or shrubs (10.8%). The mean diameter of the embraced support (i.e. liana, branch or twig) was 1.05 ± 0.12 cm (n = 33 leaves). Only two plants reached more than 5 m in height.

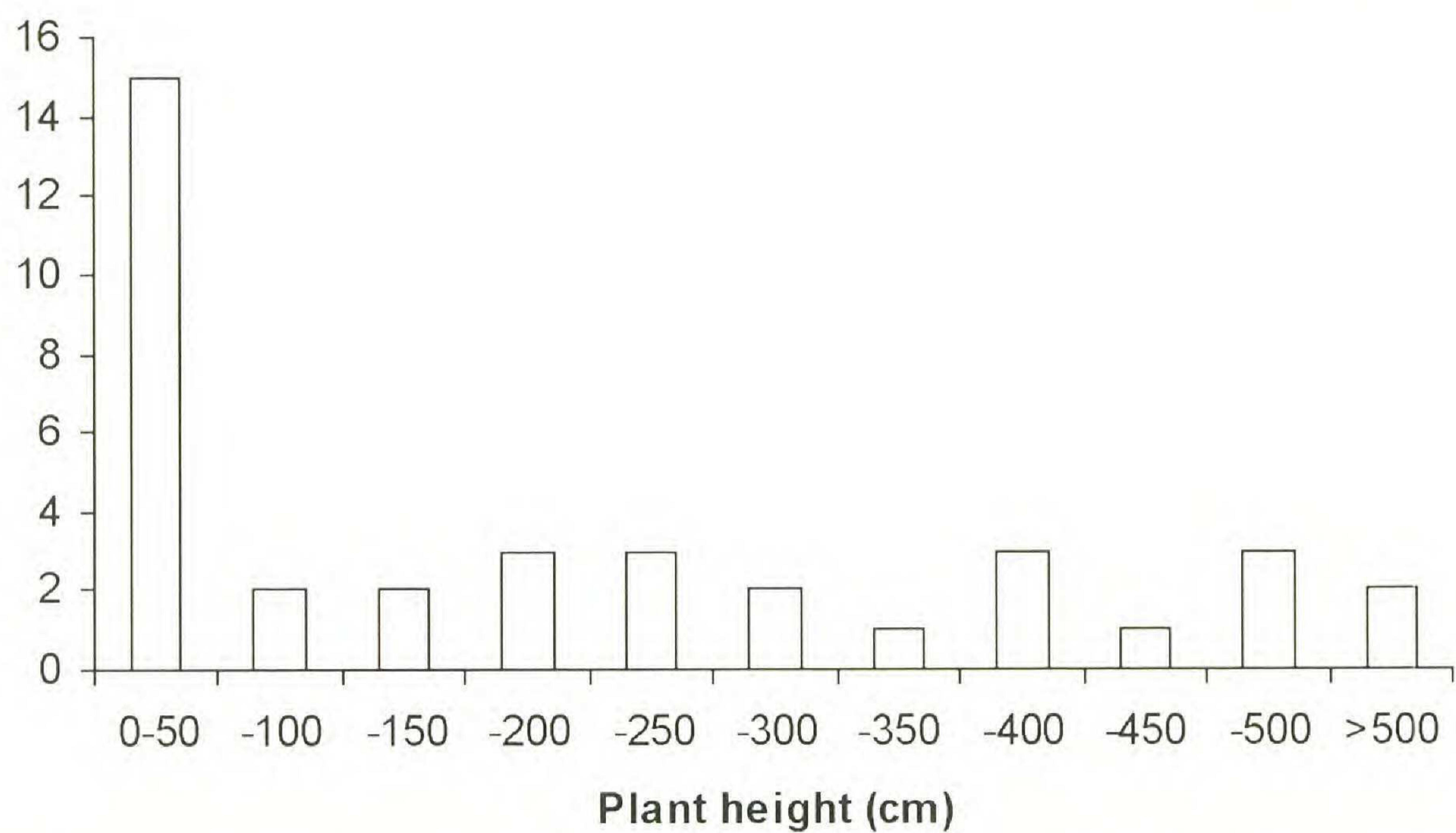


FIGURE 1. Plant height of a population of *Lygodium venustum* (n = 37) in La Mancha. Only plants of the first height class (0–50 cm) had no climbing support.

The mean leaf number of the population was 1.9 ± 0.27 per plant (n = 22). Leaves were produced at a rate of 3.7 ± 0.52 leaves per year, and died at a rate of 3.8 ± 0.63 leaves per year (Fig. 2). Their mean leaf life span was 5.6 ± 0.7 months. However, 54.3% of the leaves died within the first 3 months, whereas

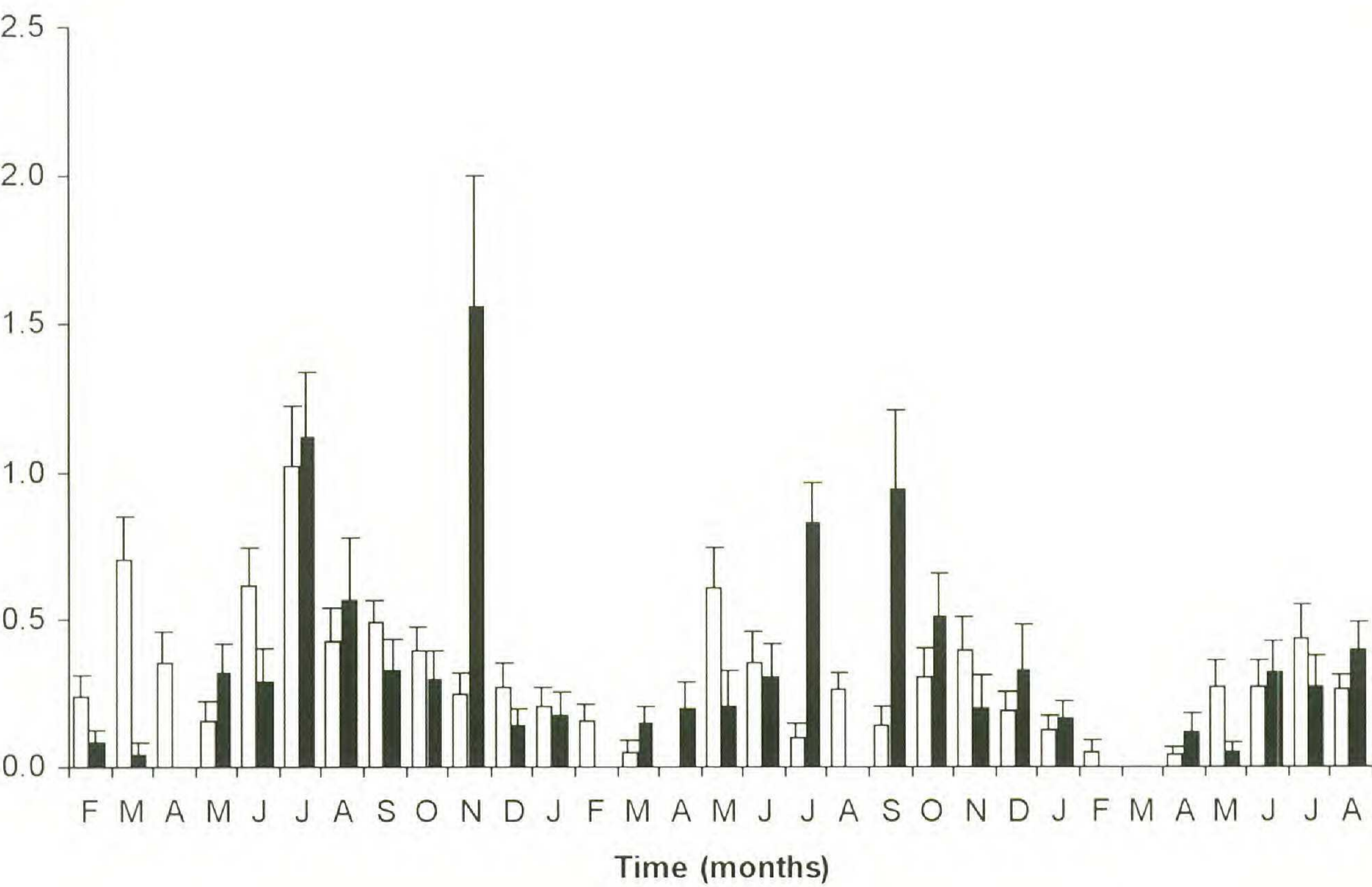


FIGURE 2. Monthly mean leaf production (white bars) and leaf mortality (black bars) of *Lygodium venustum* in La Mancha from February 1999 to August 2001. Means \pm 1 SE, n = 22.

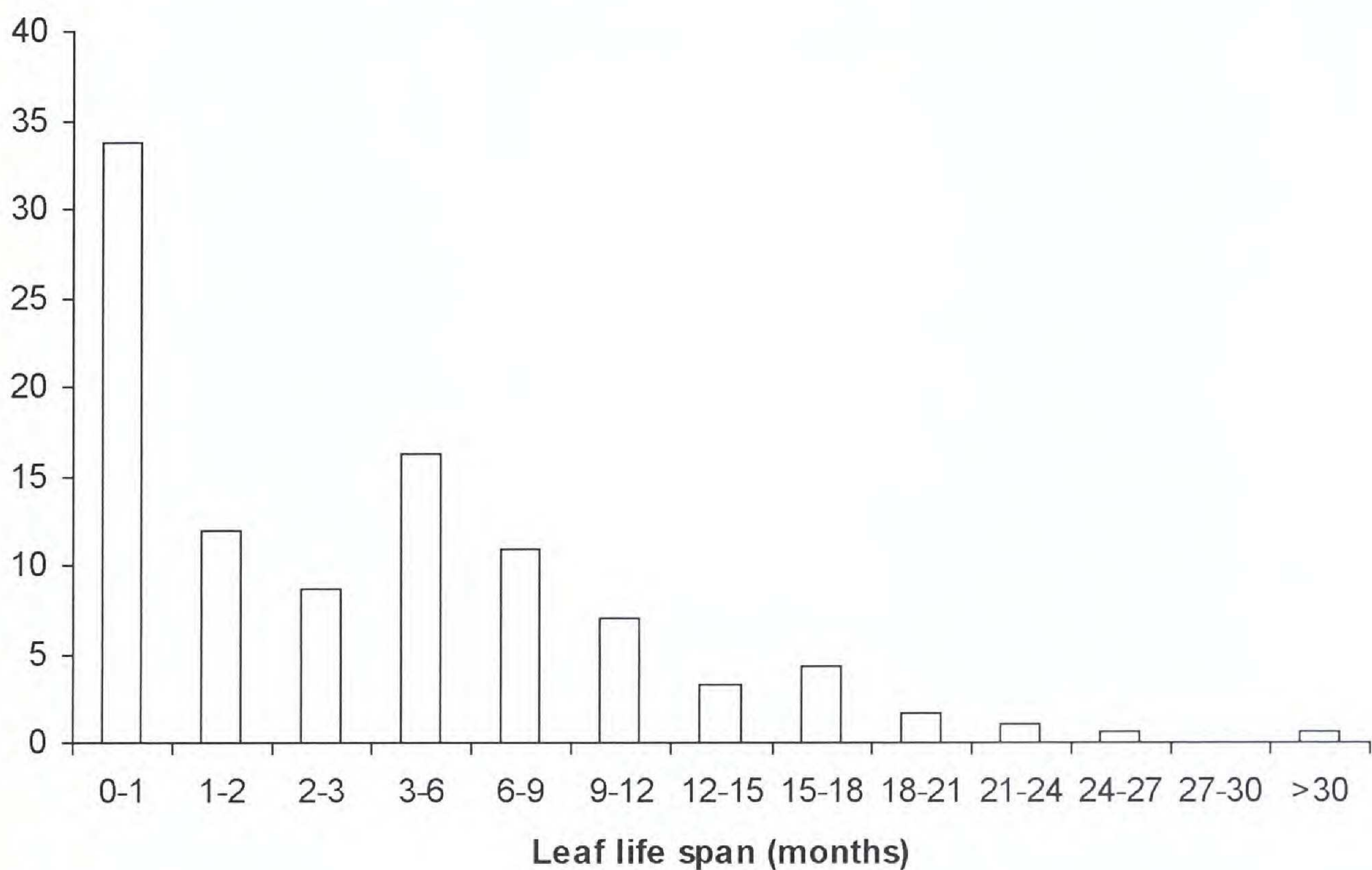


FIGURE 3. Distribution of the leaf life span of 209 leaves from 22 plants of *Lygodium venustum* in La Mancha.

11.4% lived between 12 and 30 months (Fig. 3). One leaf was alive during the entire observation period of 31 months. However, the leaf blade of the main rachis of this leaf did not stay intact, but was replaced by the leaf blades of emerging secondary axes. Leaf life span was strongly positively correlated with leaf length ($r = 0.48$, $P < 0.001$, $N = 184$). Mean leaf growth was 20 ± 5.1 cm per month. The most vigorous plant grew 85 ± 2.7 cm per month. On 17.7% of the leaves, one to five lateral buds of different levels grew out (buds of secondary axes, i.e. pinnae 11%, tertiary axes 4.3%, quaternary axes 1.4% and quinternary axes 1.0%). Such outgrowth of the lateral buds contributed 40.3% to the total leaf growth. The mean leaf length (stipe and main rachis) was 39 ± 5.7 cm. Of the 209 leaves observed, 70.3% were shorter than 50 cm, 13.4% were 50–100 cm long, 13.4% were 100–200 cm long and 2.9% were 200–600 cm long. No leaves became fertile during the observation period.

Most leaf parameters were significantly correlated among each other and with mean temperature and precipitation (Table 1, Fig. 4). Correlation coefficients between leaf parameters and precipitation were higher than between leaf parameters and mean temperature. The strongest correlation existed between leaf growth of secondary axes and precipitation. The application of a time lag series with a one-month delay increased the correlation coefficient between leaf parameters and climatic factors with the exception of leaf production and precipitation (Table 1). With a two-month delay, all correlation coefficients became smaller with the exception of the correlation between leaf mortality and mean temperature ($r = 0.69$, $P = 0.001$).

TABLE 1. Correlation coefficients between monthly population means of leaf parameters of *Lygodium venustum* in La Mancha, Gulf of Mexico, and monthly means of climatic factors during the 31-month observation period. Results of a time lag series with one month delay are given in parentheses.

	Growth (sec. axes)	Leaf production	Leaf mortality	Mean temperature	Precipitation
Growth (rachis)	0.51**	0.62***	0.39*	— (—)	— (0.46**)
Growth (secondary axes)		—	0.36*	0.42* (0.56**)	0.60*** (0.70***)
Leaf production			0.36*	0.37* (0.46**)	0.45* (—)
Leaf mortality				— (0.56**)	— (0.64**)

—, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Although leaves were produced and died during both seasons (Fig. 2), all leaf parameters differed significantly between seasons ($P < 0.05$, $df = 21$, Table 2), with the exception of leaf growth of the main rachis. Leaf growth of secondary axes and leaf mortality increased approximately threefold, and leaf production rose twofold during the rainy season from May to October (Table 2).

DISCUSSION

The studied population of *Lygodium venustum* was highly aggregated with groups of a few large plants climbing on other lianas or dead wood and several small plants without a climbing support. Nevertheless all plants were separated from each other by at least 20 cm distance. This distribution pattern should be

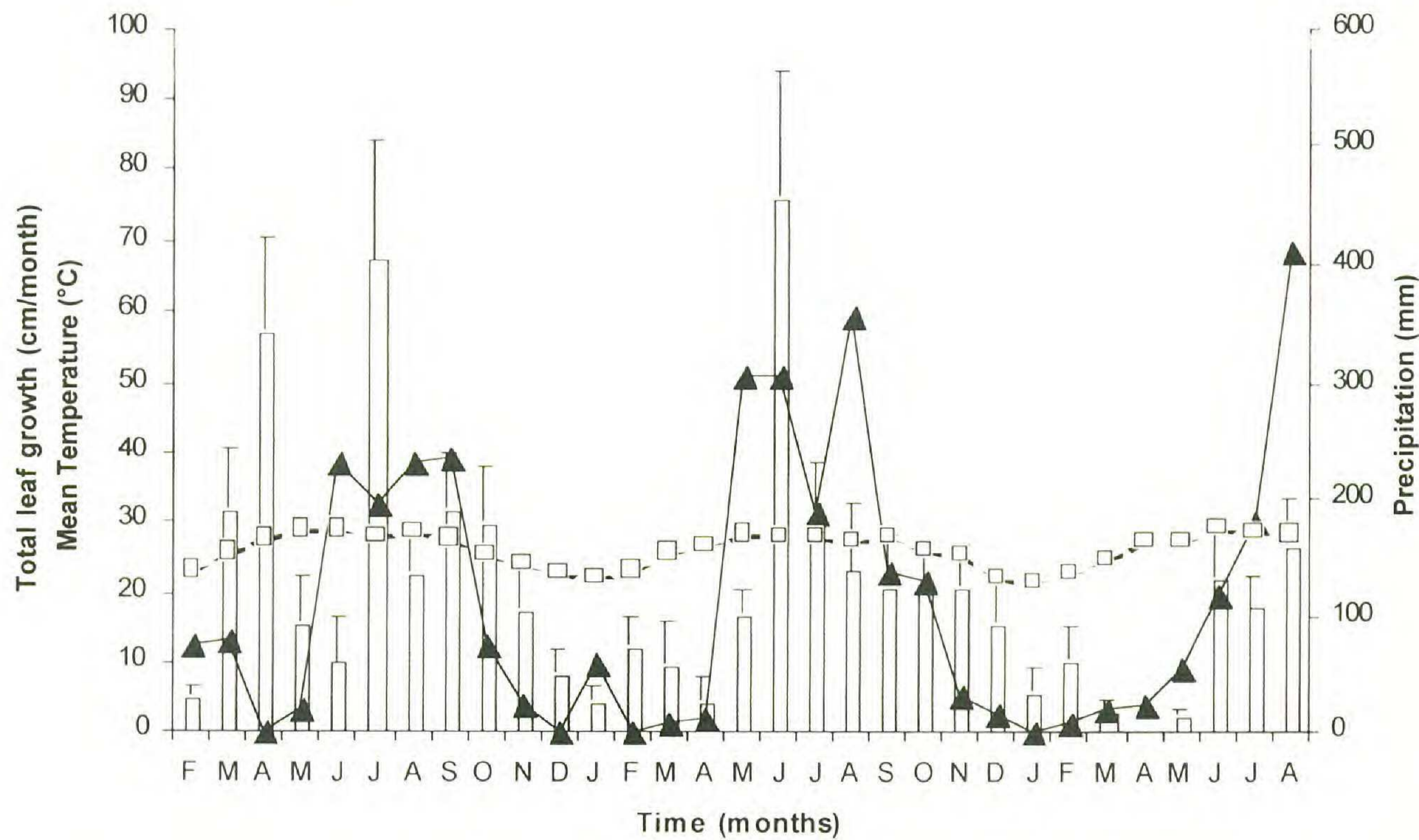


FIGURE 4. Total leaf growth (main rachis and secondary axes) of *Lygodium venustum* (bars, Means + 1 SE, $n = 22$), monthly precipitation (solid triangles) and mean temperature (open squares) in La Mancha from February 1999 to August 2001.

TABLE 2. Seasonality of leaf parameters of *Lygodium venustum* in La Mancha, Gulf of Mexico, during the 31-month observation period (paired t-test, df=21). Secondary axis growth was compared with a Wilcoxon signed rank test, because data were not normally distributed. Means \pm 1 SE.

	Dry season (Nov–Apr)	Rainy season (May–Oct)
Rachis growth (cm)	10.3 \pm 3.05	14.7 \pm 3.62
Secondary axis growth (cm)	3.57 \pm 1.66*	12.5 \pm 4.02*
Leaf production	0.20 \pm 0.04**	0.38 \pm 0.06**
Leaf mortality	0.14 \pm 0.04**	0.39 \pm 0.06**

*, $P < 0.05$; **, $P < 0.001$

expected for a pioneer species that germinates and colonizes clearings and disturbed areas where broken tree branches and lianas are frequent. The presence and persistence of small plants for over 30 months within the understory indicates a capacity for this species to maintain a living reserve awaiting presumably better light conditions similar to the persistent seedlings of several tree species.

Species of *Lygodium* have been reported as weedy and as invaders in abandoned coconut and banana plantations (Tryon and Tryon, 1982). The Old World species *Lygodium japonicum* and *L. microphyllum* were introduced in Florida, where the latter readily invades disturbed areas (Nauman and Austin, 1978; Pemberton and Ferriter, 1998). In 1999, it was estimated that *L. microphyllum* covered 107,000 acres in Florida (Langeland, 2002). Because its extensive growth presents a fire hazard, biologic control organisms have been sought (Mound, 2002).

In Mexican vanilla plantations, *L. venustum* often becomes weedy, because it finds the right light conditions and a perfect support plant (J. G. García-Franco, pers. comm.). The rhizome of *L. venustum* grows about 10 cm below soil level, branches dichotomously several times and produces new leaves near each branch tip (K. Mehlterer, pers. obs.). Plants are difficult to eradicate because when pulled, rhizomes fragment and the remaining branch tips readily regenerate new leaves. In laboratory cultures, *L. venustum* needs about three months to develop from spore to the production of a first sporophyte leaf (Mendoza *et al.*, 1999). Therefore, it cannot be considered a rapidly developing species, because its life cycle needs too much time. It would only have a chance to be a successful pioneer, if it could maintain a reserve of young sporelings in the understory. However, during the study period, neither gametophytes nor new young sporophytes were observed. This suggests that sporelings probably develop more often in newly exposed, open sites rather than in the shady understory.

It was technically impossible to take into account the largest plants on the study site (see Methods). For this reason, the results presented allow only an approximation of the leaf parameters of larger adult plants of *Lygodium venustum*. The observed smaller plants had on average two leaves and a leaf turnover of six months. The relatively short life span of the leaves must be interpreted cautiously, because most leaves died as a consequence of mechanical damage or herbivory within the first three months. The potentially most important herbivore is the land crab *Gecarcinus lateralis* (Gecarcinidae) that

frequents the *Lygodium* sites and often has caused damage to the flagging tape as well (K. Mehltreter, pers. obs.). However, larger leaves had significantly longer life spans ($r = 0.48$, $P < 0.001$, $N = 184$) of 12–31 months (Fig. 3), similar to wet forest, shade-tolerant trees (32.2 months, Coley and Aide, 1991). Longer leaves of *L. venustum* have the advantage that their sprouting dormant buds can climb the same support as the primary rachis, whereas new leaves must first find their own climbing support. For this reason dormant buds are more successful and their growth made up 40.3% of the total leaf growth although only 17.7% of the leaves developed secondary branches. In the laboratory, dormant buds of *L. japonicum* sprouted constantly 7 days after removal of the main apex (Punetha, 2000). However, under natural conditions most dormant buds of *L. venustum* seemed to lose their viability quickly or never sprouted after the death of the main apex. The leaf life span of even larger plants than in this study may be considerably longer particularly if we consider that the climbing leaves are functionally the same as the shoots of angiosperm lianas (Mueller, 1982a, 1983), but the positive xylem pressure of the roots of up to 66 kPa, which is sufficient to refill embolised tracheids up to 7 m high, may finally limit leaf growth (Ewers *et al.*, 1997). Leaf life span in ferns is quite variable and appears to be negatively correlated with leaf production (Mehltreter and Palacios-Rios, 2003). Longer life spans in fern leaves have been reported only for sterile leaves of *Danaea wendlandii* (39.6 months, Sharpe, 1993) and for the tree ferns *Alsophila salvinii* (24 months, Seiler, 1981, 1995) and *Cibotium taiwanense* (16 months, Chiou 2001). These species were also characterized by a low leaf production of 1.6, 2.5 and 2.3 leaves per year, respectively.

Surprisingly no plant became fertile during the study period. Only twice did I find fertile leaves on plants, these about 500 m from the study site; one grew in the forest and had more than 30 leaves that reached the canopy, the other was only 1.5 m high, but grew in the sun (K. Mehltreter, pers. obs.). For this reason, I suppose that direct sun light is of primary importance for the induction of fertility.

Seasonal leaf growth and leaf production is common in tropical ferns of different habitats (Mehltreter and Palacios-Rios, 2003). Most leaf parameters of *L. venustum* were seasonal and correlated with both mean temperature and precipitation especially after a time lag of one month (Table 1). All leaf parameters were more strongly correlated with precipitation than with temperature, indicating that water is a more limiting factor. In an adjacent area that is consistently wet, a population of the mangrove fern *Acrostichum danaeifolium* also showed seasonal growth patterns, but its leaf growth was more strongly correlated with temperature and there was no time lag between precipitation and leaf growth (Mehltreter and Palacios-Rios, 2003).

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